

New Glyptodont from the Codore Formation (Pliocene), Falcón State, Venezuela, its relationship with the *Asterostemma* problem, and the paleobiogeography of the Glyptodontinae

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with 3 figures

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Abstract: One of the basal Glyptodontidae groups is represented by the Propalaeohoplophorinae (late Oligocene – middle Miocene), whose genera (*Propalaeohoplophorus*, *Eucinepeltus*, *Metopotoxus*, *Cochlops*, and *Asterostemma*) were initially recognized in Argentinian Patagonia. Among these, *Asterostemma* was characterized by its wide latitudinal distribution, ranging from southernmost (Patagonia) to northernmost (Colombia, Venezuela) South America. However, the generic assignation of the Miocene species from Colombia and Venezuela (*A.?* *acostae*, *A. gigantea*, and *A. venezolensis*) was contested by some authors, who explicitly accepted the possibility that these species could correspond to a new genus, different from those recognized in southern areas. A new comparative study of taxa from Argentinian Patagonia, Colombia and Venezuela (together with the recognition of a new genus and species for the Pliocene of the latter country) indicates that the species in northern South America are not Propalaeohoplophorinae, but represent the first stages in the cladogenesis of the Glyptodontinae glyptodontids, the history of which was heretofore restricted to the late Miocene – early Holocene of southernmost South America. Accordingly, we propose the recognition of the new genus *Boreostemma* for the species from northern South America and the restriction of *Asterostemma* to the Miocene of Patagonia. Thus, the available data indicate that the Glyptodontinae would in fact have arisen in the northernmost regions of this continent. Their arrival to more southerly areas coincides with the acme of the “Age of Southern Plains”. The Propalaeohoplophorinae are geographically restricted to Patagonia.

Keywords: *Boreostemma pliocena* n. gen., n. sp. • Glyptodontinae • Propalaeohoplophorinae • paleobiogeography • phylogeny • South America

Kurzfassung: Eine der basalen Gruppen der Glyptodontidae stellen die Propalaeohoplophorinae (spätes Oligozän – mittleres Miozän) dar, deren Gattungen (*Propalaeohoplophorus*, *Eucinepeltus*, *Metopotoxus*, *Cochlops* und *Asterostemma*) man zuerst aus dem argentinischen Patagonien kannte. Darunter ist *Asterostemma* durch eine weite latitudinale Verbreitung gekennzeichnet, welche sich vom südlichsten (Patagonien) zum nördlichsten (Kolumbien, Venezuela) Südamerika erstreckt. Allerdings wurde die Gattungszugehörigkeit der miozänen Arten Kolumbiens und Venezuelas (*A.?* *acostae*, *A. gigantea* und *A. venezolensis*) von einigen Autoren angezweifelt, die explizit die Möglichkeit in Betracht zogen, dass diese Taxa einer anderen Gattung angehören, die sich von der Gattung der südlichen Breiten unterscheidet. Ein neuer Vergleich der Taxa aus Patagonien, Kolumbien und Venezuela (zusammen mit einer neuen Gattung und Art aus dem Pliozän Venezuelas) zeigt, dass die Arten aus dem nördlichen Südamerika nicht zu den Propalaeohoplophorinae gehören, sondern die ersten Stufen in der Kladogenese der glyptodontinen Glyptodontidae darstellen. Deren Geschichte war bislang auf das späte Miozän – frühe Holozän des südlichsten Südamerikas beschränkt. Dementsprechend stellen wir hier die neue Gattung *Boreostemma* für die Arten des nördlichen Südamerikas auf; *Asterostemma* wird auf das Miozän Patagoniens beschränkt. Die Datenlage deutet somit darauf hin, dass Glyptodontinae sich tatsächlich im nördlichsten Teil Südamerikas entwickelten. Ihr Auftreten in den südlichen Gebieten fällt mit dem Höhepunkt des „Zeitalters der südlichen Ebenen“ zusammen. Die Verbreitung der Propalaeohoplophorinae wird geographisch auf Patagonien beschränkt.

Schlüsselwörter: *Boreostemma pliocena* n. gen., n. sp. • Glyptodontinae • Propalaeohoplophorinae • Paläobiogeographie • Phylogenie • Südamerika

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Introduction

Among the particular palaeofauna that inhabited South America during much of the Cenozoic, the cingulate superfamily Glyptodontoidea are one of the most conspicuous groups; several authors have recognized more than 65 genera during their diversification (late Eocene – early Holocene) (see MCKENNA & BELL 1997). In this context, the Glyptodontidae Propalaeohoplophorinae (sensu CASTELLANOS 1932) are among the best characterized basal clades (together with the Glyptatelinae; late Eocene – late Miocene; SCILLATO-YANÉ 1977; CARLINI et al. 1997; VIZCAÍNO et al. 2003), and have been proposed by several authors as potential structural ancestors of later Glyptodontidae (SCOTT 1903–1904; SCILLATO-YANÉ 1977).

The propalaeohoplophorine glyptodonts are morphologically characterized by the following traits: a) low elongated skull, partly resembling those of dasypodid cingulates; b) dorsal carapace with mobile bands on the lateral margins (no less than 6 rows in *Propalaeohoplophorus* and *Cochlops*), which is probably the primitive condition for the Glyptodontidae; c) ornamentation of dorsal carapace osteoderms consisting of a polygonal central figure completely encircled by a row of smaller peripheral figures, forming a rosette; d) caudal armor formed by a series of rings (generally four to six), each ring formed by two rows of osteoderms, followed by a short caudal tube; e) five digits in both fore- and hindlimbs; f) first three upper and lower molariforms simple, subcircular or subelliptic in transversal section. Many of these characters could be considered primitive; however, some of them (c–d) do not occur in the Glyptatelinae, or there is no evidence of their occurrence.

From a chronological viewpoint, the subfamily Propalaeohoplophorinae is first recorded during the Deseadan (late Oligocene) (SCILLATO-YANÉ 1977), a time of remarkable increase in glyptodontid diversity. The Deseadan also marks the end of the records of Glyptatelinae at high latitudes; however, they persist in more northern areas, until the middle Miocene in Colombia (CARLINI et al. 1997; VILLARROEL & CLAVIJO 2005) and until the late Miocene in Uruguay (VIZCAÍNO et al. 2003). They might even have occurred in the early Pleistocene of North America (MCKENNA & BELL 1997).

During the Colhuehuapian (early Miocene), and especially during the Santacrucian (early Miocene), the Propalaeohoplophorinae show great diversification, evidenced in the recognition of five genera and eight species in Argentinian Patagonia during this latter South American Land Mammal Age (SALMA): *Propalaeohoplophorus* AMEGHINO, 1887 (*P. australis* and *P. minor*), *Cochlops* AMEGHINO, 1889 (*C. muricatus* and *C. debilis*), *Eucinepeltus* AMEGHINO, 1891 (*E. complicatus* and *E. petestatus*), *Metopotoxus* AMEGHINO, 1898 (*M. anceps*), and *Asterostemma* AMEGHINO, 1889 (*A. de-*

pressa) (see SCOTT 1903–1904). In this context, a recent phylogenetic analysis of the southern Propalaeohoplophorinae (*Propalaeohoplophorus*, *Eucinepeltus*, *Metopotoxus*, and *Cochlops*) has suggested that these taxa can be regarded as a monophyletic group (FERNÍCOLA 2006).

The “Friasian” lapse (middle – late Miocene) (which comprises three successive “faunas”, Friasian s. s., Colloncuran and Mayoan; SCILLATO-YANÉ & CARLINI 1998) signals the beginning of the Panaraucarian Faunal Cycle, Protoaraucarian Subcycle (Friasian – Chasicuan, of PASCUAL & ORTIZ JAUREGUIZAR 1990; PASCUAL et al. 1996). The Xenarthra, especially the large cursorial Tardigrada (such as Megatheriidae, Mylodontidae, and Scelidotheriinae; see MC DONALD 1987) become larger and more frequent during this period (PASCUAL et al. 1996; ORTIZ JAUREGUIZAR & CLADERA 2006). This phenomenon could be associated with the progressive aridization of the Southern Cone of South America, as a consequence of the Andean-Patagonian Orogeny (see PASCUAL & BONDESIO 1982; PASCUAL 1984; PASCUAL et al. 1984; ORTIZ JAUREGUIZAR & CLADERA 2006; TONNI & CARLINI in press). This climatic-environmental context characterizes the last southern records of Propalaeohoplophorinae (*Propalaeohoplophorus*? and *Eucinepeltus*) (BONDESIO et al. 1980), as well as the first records of Hoplophorinae, with the tribes Hoplophorini? (*Eonaucum colloncuranun* SCILLATO-YANÉ & CARLINI, 1998) and Palaeohoplophorini (*Palaeohoplophorus* AMEGHINO and *Palaeohoplophoroides* SCILLATO-YANÉ & CARLINI) (PAULA COUTO 1979; SCILLATO-YANÉ & CARLINI 1998).

Argentinian Patagonia seems to have been, at least until the “Friasian” (middle to late Miocene), the geographic location where the cladogenesis and radiation of this group is best recorded (PASCUAL & ODREMAN RIVAS 1973; PASCUAL et al. 1984), considering the good record of cingulates in the area (SCILLATO-YANÉ 1986). Furthermore, PASCUAL et al. (1984) and PASCUAL & ODREMAN RIVAS (1973) went so far as to propose this territory as a center of radiation and cladogenesis.

Recently, other possible evolutionary scenarios have been proposed for the Cingulata at lower latitudes. These hypotheses are especially supported by fossil remains from the Honda Group (“Friasian”) in the fossil locality of La Venta, Colombia (CARLINI et al. 1997). Several taxonomic and paleobiogeographic differences between these materials and isochronous Patagonian paleofaunas support these hypotheses. These include the remarkable survival of a representative of the glyptateline Glyptodontidae (*Neoglyptatelus originalis*) with very primitive characters (CARLINI et al. 1997), as well as records of astegotheriine, dasypodine, and tolpeutine Dasypodidae, which are absent in Patagonia; in contrast, representatives of Peltephilidae, Euphractini, and Stegotheriini occur in the latter region (CARLINI et al. 1997).

Within this paleobiogeographic context, the Mio-Pliocene glyptodontid fauna in northern South America (Colombia and Venezuela), which remained unknown until the mid-1940s (see SIMPSON 1947), seems to agree with this hypothesis. Traditionally, all the Miocene glyptodonts from this area were included within the subfamily Propalaeohoplophorinae, and more precisely, within the genus *Asterostemma*. Thus, three species have been described, *A. venezolensis* SIMPSON, 1947, for the (middle?) Miocene of Venezuela, and *A. ? acostae* VILLARROEL, 1983 and *A. gigantea* CARLINI et al., 1997, for the middle Miocene (Laventan SALMA) of Colombia. The inclusion of these taxa in the southern genus *Asterostemma* was accepted by most authors, though with the explicit acknowledgment that these taxa could in fact represent a new genus, different from the ones traditionally recognized for the Patagonian Miocene (i.e., *Propalaeohoplophorus*, *Eucinepeltus*, *Metopotoxus*, *Cochlops*, and *Asterostemma*) (see SIMPSON 1947: 9; VILLARROEL 1983: 30; CARLINI et al. 1997: 223).

In this contribution we present a new Glyptodontidae from the Codore Formation (Pliocene) of Falcón State, Venezuela (Fig. 1); concurrently, on the basis of both morphological and paleobiogeographic evidence, we propose the recognition of a new genus for all the Mio-Pliocene species recognized in northern South America (Colombia and Venezuela) that have tentatively been assigned to the southern genus *Asterostemma*.

The new Glyptodontidae described herein allows the proposal of a different evolutionary scenario for the species from northern South America; particularly, it allows us to elaborate a different hypothesis for the differentiation of the glyptodontine Glyptodontidae. This subfamily is known from the “Araucanian” (late Miocene – Pliocene) of NW Argentina, represented by *Glyptodontidium tuberifer* CABRERA, 1944, a species with dorsal carapace formed by thick osteoderms with the typical rosette comprising a central polygonal figure and several marginal figures in a single row. Although this character would be primitive among the propalaeohoplophorine and glyptodontine glyptodonts, the morphology of the sulci that delimit the pattern on the exposed surface of the osteoderms is different in cross section. While in the southern Propalaeohoplophorinae the cross section of these sulci is parabolic (“V”-shaped), in the Glyptodontinae it is quadrangular (“U”-shaped), with almost vertical sides and a wide, almost flat bottom. In addition, the carapace osteoderms of glyptodontines are relatively thicker than those of propalaeohoplophorines, and the contact edges between successive osteoderms are definitely denticulated. In general, the section of these sulci and the thickness of osteoderms, together with the greater lobation of the anterior molariforms, are generally used to define the glyptodontine glyptodonts (HOFFSTETTER 1958; PASCUAL et al. 1966; PAULA COUTO 1979).

The history of the Glyptodontinae is rather particular, given that their earliest records (*Glyptodontidium tu-*

berifer from the “Araucanian”; late Miocene – Pliocene) are not very frequent or diverse in late Neogene sediments; only two species, *Paraglyptodon chapalmalensis* from the middle Pliocene (Chapadmalalan) of the Pampean region and *Paraglyptodon uquiensis* CASTELLANOS, 1953, from the middle – late Pliocene (late Chapadmalalan – Sanadresian) of the current territory of Jujuy province (see REGUERO et al. 2007), both from Argentina, have been described for that period. However, the Glyptodontinae become very frequent in southern sediments since the Ensenadan (late Pliocene – early Pleistocene; ca. 1.7 – 0.98 Ma) of the Pampean region, achieving both noticeable taxonomic richness and extensive latitudinal distribution that ranged from the south of Buenos Aires province to, probably, Venezuela (see MARSHALL et al. 1984; TONNI & SCILLATO-YANÉ 1997; RINCÓN 2006). Thus, approximately eight *Glyptodon* species have been recognized for the Pleistocene of southernmost South America (SOIBELZON et al. 2006; CARLINI & SCILLATO-YANÉ 1999).

Similarly, this subfamily is very well represented in North America since the early Blancan (ca. 2.6 Ma), that is, immediately after the establishment of a continuous Panamanian terrestrial connection (ca. 2.7 Ma), with the genus *Glyptotherium* (see CARLINI et al. 2008). However, recently CARRANZA-CASTAÑEDA & MILLER (2004) cited the presence of *Glyptotherium* OSBORN, 1903 in Pliocene sediments from central Mexico, dated by them at 3.9 Ma, although the generic assignment is not secure, given that the authors themselves (2004: 258) highlight the marked differences with respect to known *Glyptotherium* species. It would not be surprising, if these Mexican findings were to correspond in fact to a new taxon close to the one described here.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; M, m, upper and lower molariform respectively; GABI, Great American Biotic Interchange; ICNUNC, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; IGM, Instituto de Geociencias y Minería, Colombia; n/n, without official catalog number; SALMA, South American Land Mammal Age.

Geologic and stratigraphic context: the Codore Formation

The Codore Formation was recognized and described by HODSON (1926) in Falcón State, Venezuela, and assigned chronologically to the Pliocene s.l., while always considered older than the overlying San Gregorio Fm. from the late Pliocene (GONZALEZ DE JUANA et al. 1980). This geologic unit is divided into two (see LIDDLE 1946) or three (see REY 1990) members, according to different authors. Lithologically, it comprises a succession of ochraceous to dark brown sandstones with cross-stratification, and light-colored limolites with in-



Fig. 1. Map showing the locality where the type specimen of *Boreostemma pliocena* n. gen., n. sp. was recovered.

tercalated carbonatic levels of varying thickness. The depositional environment has been interpreted by REY (1990) as characteristic of a distal fan-delta, with an alluvial plain associated with small meandering channels, and some brief intervals of marine invasion halfway through the sequence. The presence of palynomorphs allows to infer subhumid to dry climate throughout the entire deposition of the Codore Fm. (LINARES 2004). The sequence is about 800 m thick and comprises sediments concordant with the underlying Urumaco Fm. (late Miocene). Recently, LINARES (2004), on the basis of the mammalian fauna, has assigned an age corresponding to the Montehermosan SALMA (late Miocene – early Pliocene) to the El Jebe Member of Codore Fm., and suggested a probable age of 6 Ma for the contact between the Urumaco and Codore formations.

Systematic paleontology

Xenarthra COPE, 1889
 Cingulata ILLIGER, 1811
 Glyptodontoidea GRAY, 1869
 Glyptodontidae GRAY, 1869
 Glyptodontinae GRAY, 1869

Boreostemma n. gen.

Etymology: *Boreos* from the Latin “borealis” “from the North”, in reference to its geographical distribution, restricted to northern South America, + “*stemma*” ending of *Asterostemma*, austral genus to which it was previously wrongly assigned.

Type species: *Boreostemma pliocena* n. gen., n. sp., from the Codore Formation, El Jebe Member, Pliocene, northern Venezuela.

Referred species: The type species and *Asterostemma venezolensis* SIMPSON, 1947 (middle? Miocene, eastern Venezuela), *Asterostemma? acostae* VILLARROEL, 1983 [sic]

(middle Miocene, Huila Department, Colombia), *Asterostemma gigantea* CARLINI et al., 1997 (La Victoria Formation, Honda Group, middle Miocene; Huila Department, Colombia).

Diagnosis: Small to medium sized Glyptodontinae, ranging in size from that of *Propalaeohoplophorus australis* to *Eucinepeltus crassus*. Osteoderms arranged in transverse bands more regular than in Propalaeohoplophorinae, with rugose and very punctate surface. Central figure polygonal, in a more central position. Sulci surrounding adjacent figures wide, which has (in cross section) nearly vertical walls and wide bottom, which we call "U"-shaped, contrasting with the "V"-shaped sulci of Propalaeohoplophorinae and Hoplophorinae hoplophorini with convergent walls and strait bottom. Area of contact and articulation of adjacent osteoderms strongly denticulate, with deep osseous interdigitating projections. Generally, a single series of peripheral figures in each osteoderm, morphologically simpler than those of Glyptodontidae Propalaeohoplophorinae. Peripheral figures of two or three adjacent osteoderms forming composite figures. Caudal rings imbricated, formed by a single row of osteoderms. Posterior region of caudal tube with slightly imbricated osteoderms, more similar to the caudal tube of Dasypodidae than to those of known Propalaeohoplophorinae. Dorsal carapace formed by larger, thicker and fewer osteoderms than in Propalaeohoplophorinae.

***Boreostemma pliocena* n. sp.**

Figs. 2A–D, 3

Etymology: "*pliocena*" from Pliocene, the age of the Codore Formation, Venezuela.

Holotype: Thirty complete, associated osteoderms, some fragmentary osteoderms, and a fragment of the palate with partial alveoli of M 5–7.

Type locality: Road to Tío Gregorio locality, Urumaco, Estado Falcón, Venezuela, 11° 15' 35" N and 70° 17' 30" W (Fig. 1).

Stratigraphic range and geochronologic age: El Jefe Member of the Codore Formation, Pliocene.

Diagnosis: Osteoderms of dorsal carapace very large, with extremely punctuate dorsal surface, very similar in this respect to *Boreostemma gigantea*, *B. acostae*, *B. venezolensis*, *Glyptodontidium tuberifer* and *Paraglyptodon uquiensis*, and contrasting with the condition observed in the southern Propalaeohoplophorinae (*Propalaeohoplophorus*, *Eucinepeltus*, *Metopotoxus*, and *Asterostemma*), which have a smoother exposed surface. Punctuation especially concentrated in a slight central concavity at each central figure, more visible in the largest (dorsal and posterodorsal) osteoderms. Sulci dividing the central figure from the peripheral ones, and the latter from each other, wide and shallow, as in *Glyptodontidium tuberifer*, *Paraglyptodon uquiensis* and *P. chapalmalensis*; hair follicle (?) pits well developed and situated (as in most of the Glyptodontidae with this rosette ornamentation pattern) at the intersections be-

tween the sulcus surrounding the central figure and the sulci between peripheral figures. Caudal rings imbricated, formed by a single row of osteoderms. Caudal ring osteoderms with barely marked central figure and without signs of peripheral figures, differing from *Propalaeohoplophorus australis* and *Cochlops muricatus* (propalaeohoplophorines whose osteoderms are well-known), in which the central figure is clearly visible and a row of peripherals is present at the proximal edge. Posterior upper molariforms (at least M5–M7) very close to each other, with almost no separation, differing from those of Propalaeohoplophorinae, in which the separation between molariforms increases disto-proximally. Ornamentation of cephalic shield osteoderms similar to that of dorsal carapace, as in *Propalaeohoplophorus australis* and the hoplophorine Hoplophorinae *Neosclerocalyptus* PAULA COUTO, 1957, and very different from that of *Eucinepeltus complicatus* and *Metopotoxus laevatus*, which show no signs of rosette ornamentation.

Description and assignation of material

Palate: This is a posterior fragment with part of the alveoli for molariforms M6 and M7 on the left side, and the last alveolar lobe of M6, that of M7 and the first of M8 on the right side (Fig. 3). It is 53.5 mm long and 35 mm wide. The entire surface of the palate is pierced by foramina that are particularly evident on the midline. There are also six large foramina at the level of the first lobe of M7, at the limit between M7 and M8, and at the limit between the first and second lobes of M8. On the right side, these foramina open at the level of the last lobe of M6, the second lobe of M7 and the first lobe of M8. Apart from this, the particular arrangement of the alveoli for the last molariforms shows virtually no separation between M7 and M8. This trait is clearly different from the condition in Propalaeohoplophorinae, in which the separation between successive molariforms increases disto-proximally. On the other hand, the middle lobe seems to be more inclined with respect to the longitudinal axis of the palate than in *Propalaeohoplophorus*, *Asterostemma*, *Eucinepeltus*, and *Cochlops*, in which this lobe is approximately at straight angles to the anteroposterior axis of the dental series.

Osteoderms: Numerous osteoderms from the dorsal carapace, as well as some from the cephalic shield, have been preserved. They are categorized into five groups according to their location on the dorsal carapace.

a) First group: these osteoderms correspond to the dorsal or postero-dorsal region of the carapace (Fig. 2A). The larger ones are 51 mm by 47 mm in diameter, and 14 mm thick, while the smaller are 39 mm by 33 mm and 10 mm, respectively. Each osteoderm has five or six sides (in most) which are relatively isodiametric, with extremely punctate dorsal surface, as in *Glyptodontidium tuberifer*, *Paraglyptodon uquiensis*, and *Boreostemma acostae* (n. comb.). The central figure is poly-

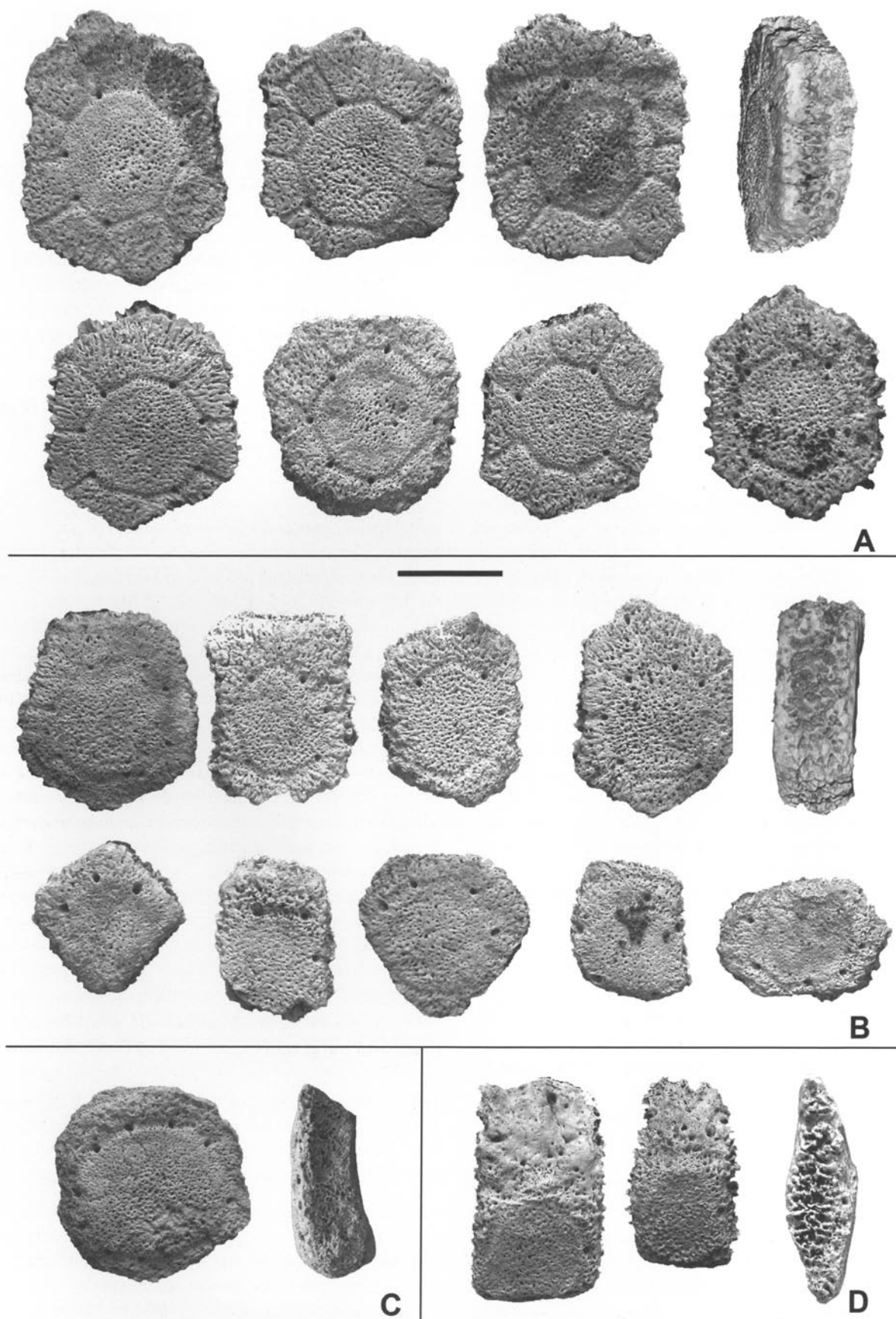


Fig. 2. *Boreostemma pliocena* n. gen., n. sp. **A:** Osteoderms corresponding to the dorsal or postero-dorsal region of the carapace (seven in external view, one in lateral view). **B:** Osteoderms from the sides of the carapace (nine in external view, one in lateral view). **C:** One osteoderm from the cephalic shield (external and lateral views). **D:** Osteoderms from the caudal rings (two in external view, one in lateral view). – Scale bar = 2 cm.

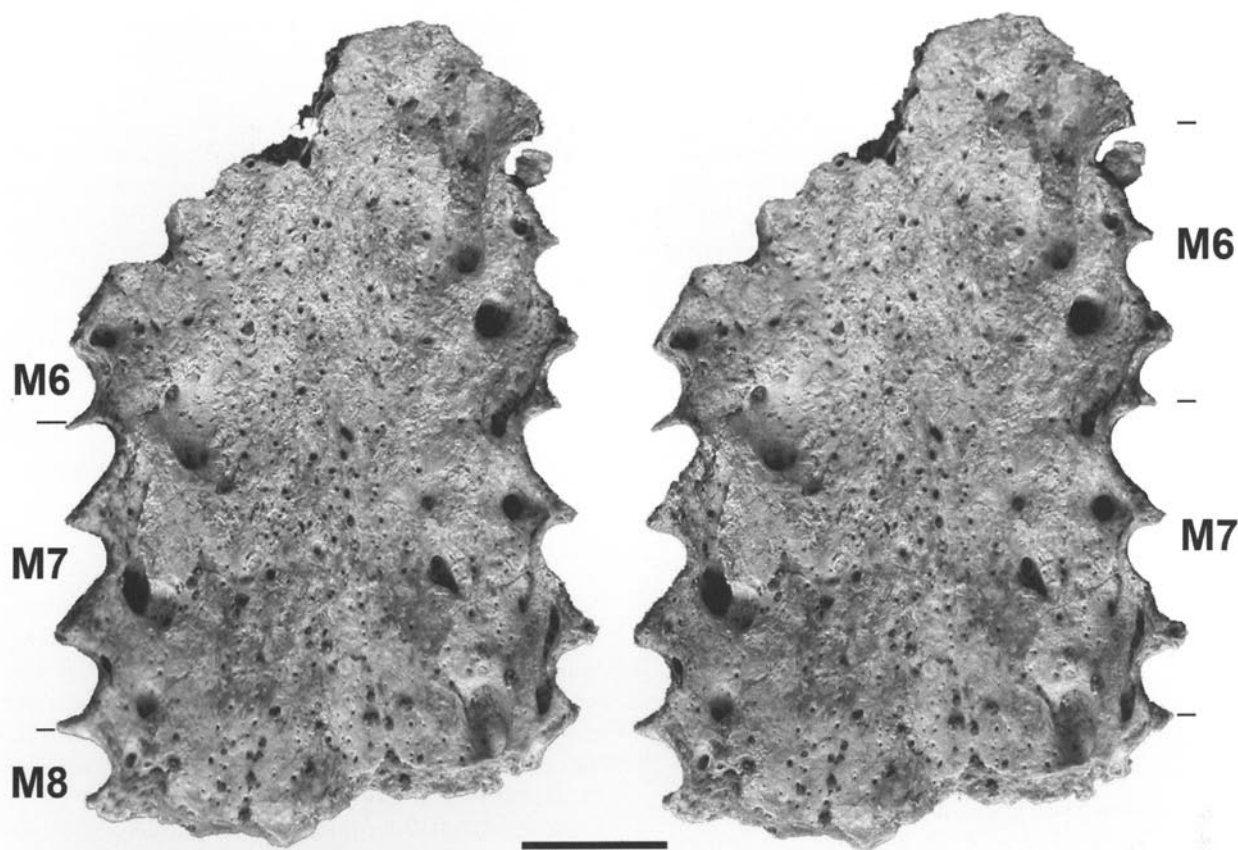


Fig. 3. *Boreostemma pliocena* n. gen., n. sp. Palate: stereopairs of a posterior fragment with part of the alveoli for molariforms M6 and M7 on the left side, and the last alveolar lobe of M6, that of M7 and the first of M8 on the right side. — Scale bar = 2 cm.

gonal, with the number of sides coinciding with the number of peripheral figures. The central figures of the larger osteoderms are between 23.5 by 21 mm, and 25 mm by 19 mm. The figures of the smaller osteoderms are 19 mm by 18 mm. The dorsal surface of the central figures is slightly elevated with respect to the peripheral ones, particularly in the larger osteoderms, whereas it is flat in the smaller ones. As mentioned above, the entire surface of each central figure is densely punctate (although much less than in *Glyptodon* and *Glyptotherium*, in which the surface of the osteoderms is definitely rugose), but this condition becomes especially evident at its central area, which bears larger-diameter foramina located in a small concavity, somewhat similarly to the morphology of *Boreostemma acostae*. As in the previous case, this concavity is more conspicuous in the larger osteoderms. Each central figure is surrounded by a row of eight to ten peripherals, 4- or 5-sided, well developed and very angular. The number of peripherals seems to be lower when compared to the southern Propalaeophlorinae forms; the latter may have up to twelve or thirteen peripherals (see SCOTT 1903–1904). The entire surface of these figures is clearly punctate, although the punctuations situated toward the periphery are somewhat radial in appearance (as they become oblique instead of perpendicular to the surface), as observed in some osteoderms of *Paraglyptodon uquiensis* and *Pa-*

raglyptodon chapalmalensis (see ROVERETO 1914; CASTELLANOS 1953). A conspicuous foramen appears in some of the intersections between the sulcus that delimitates the central figure and the radial sulci; there are three to eight of these foramina. The sulci separating the central figure from the peripherals, and the radial sulci between peripherals are wide, shallow, with nearly flat bottom, and morphologically similar to those of *Glyptodontidium tuberifer*. The sulci are similar in *Paraglyptodon uquiensis* and *P. chapalmalensis*, although in these latter species the sulci are deeper and somewhat similar to those of the genera *Glyptodon* and *Glyptotherium*.

The ventral surface of the osteoderms may be flat or slightly concave at the center. One to nine foramina are visible on this surface; generally the largest (one or two of them) occupy a central position while the rest are arranged peripherically in a circular pattern.

b) Second group: osteoderms from the sides of the carapace (Fig. 2B). These are rectangular with a disto-proximal long axis, and have four to six sides. The largest are 37.5 mm by 23 mm and 14 mm thick, while the smallest are 28 mm by 21 mm and 9.5 mm thick. The entire exposed surface is visibly punctate, as in the dorsal and posterodorsal osteoderms. The central figure is flat, with subelliptical to subcircular outline, and unlike the dorsal osteoderms, does not show a concave area with larger fo-

ramina. The eight or nine peripheral figures are less developed than in the dorsal osteoderms, and the lateral ones are smaller. As in the Propalaeohoplophorinae and the most primitive hoplophorine Hoplophorinae (i.e., *Eosclerocalyptus tapinocephalus* and *E. proximus*), the anterior peripheral figures are larger than the posterior ones. The central and radial sulci are only slightly marked, and the number of foramina ranges between three and six.

c) Third group: formed by very small osteoderms of the dorsal carapace, possibly corresponding to the extreme antero-lateral and postero-lateral regions of the carapace. These osteoderms are quadrangular to hexagonal, and measure from 24 mm by 24.5 mm and 11 mm thick, to 25 mm by 23 mm and 8.5 mm thick. The entire dorsal surface has the same characteristics described above for other osteoderms, with three to five well-developed hair follicle (?) pits at the intersections between the sulcus surrounding the central figure and the sulci between peripheral figures, but in this case there is no differentiation between central and peripheral figures.

d) Fourth group: osteoderms from the caudal rings (Fig. 2D). These are clearly rectangular with a disto-proximal long axis. The largest osteoderms are 44 mm by 23.5 mm and 12 mm thick, while the smallest one is 34 mm by 20 mm and 9 mm thick. Each osteoderm shows two well-defined areas: a distal area with a flat exposed surface, and a proximal area with an extremely rugose irregular surface, the latter corresponding to the area of contact and articulation with the adjacent osteoderm. The surface of the distal area is flat and punctate, although a disto-proximally elongated small convexity was observed in the center of one of the osteoderms studied. In addition, these osteoderms bear a very weak sulcus that delimits a subcircular central figure, although there are no peripheral figures; this central figure is 16 mm long by 15 mm wide in the smallest osteoderms and 19 by 17 mm in the largest ones. This particular morphology differentiates this taxon from *Propalaeohoplophorus australis* and *Cochlops muricatus*, as both have a clearly visible central figure and a row of peripherals at the proximal margin. A series of foramina, larger than those of the dorsal carapace osteoderms, is evident at the lateral and posterior margins.

Likewise, the proximal contact area is depressed toward its proximal end, and has a very rugose surface with large foramina. In lateral view, the osteoderms are maximally thick at their center and become thinner toward the edges, particularly at the proximal margin.

e) Fifth group: only one osteoderm from the cephalic shield is well preserved. It is somewhat similar to those of *Propalaeohoplophorus*, and clearly different from those of *Eucinepeltus* and *Metopotoxus* (Fig. 2C). The osteoderm is relatively isodiametric, 36 mm by 35 mm and 13 mm thick. The central figure is subcircular (24 mm by 27 mm) and slightly elevated with respect to

the peripheral figures. As in the largest dorsal carapace osteoderms, the largest punctuations are concentrated in the center of the figure, although with a slight tendency to occupy one of the margins. The twelve peripheral figures are asymmetrically developed, and largest and thickest at the margin/border. Eleven hair follicle (?) pits are clearly visible.

The ventral surface of the osteoderm is notably concave at its center; much more so than any osteoderm from the first group, with three large foramina at the area of maximum thickness.

The problem of the genus *Asterostemma* AMEGHINO in the context of the Glyptodontidae / Propalaeohoplophorinae

All the genera of propalaeohoplophorine Glyptodontidae (*Propalaeohoplophorus*, *Asterostemma*, *Cochlops*, *Metopotoxus*, and *Eucinepeltus*) were originally recognized on the basis of materials exhumed from the early and middle Miocene (Colhuehuapan, Santacrucian, and Friasian ages) of Argentinian Patagonia (see AMEGHINO 1889, 1891; LYDEKKER 1894; SCOTT 1903–1904; RUSCONI 1946, among others). Osteoderm ornamentation in this subfamily is characterized by a central figure encircled by a row of more-or-less angular peripheral figures, producing a characteristic rosette pattern (HOFFSTETTER 1958; PAULA COUTO 1979) that remains almost unchanged in later groups (e.g., hoplophorine Hoplophorinae; see ZURITA et al. 2005). This situation, together with the absence of isochronic records in more northern areas, led some authors to suggest that some of these Propalaeohoplophorinae were the ancestral stock for the remaining Glyptodontidae lineages (SCOTT 1903–1904: 155). The diagnostic characters provided by AMEGHINO (1889: 822) for his genus *Asterostemma* seem to be highly variable within a single dorsal carapace, and occur also in the remaining Propalaeohoplophorinae species (e.g., number of sides of osteoderms in the dorsal carapace, size of the central figure and development of peripheral figures). Later, SCOTT (1903–1904), as part of a systematic revision of Propalaeohoplophorinae, upheld the validity of the genus, but recognized only one of the three species originally described by AMEGHINO (1889), namely *A. depressa*, as valid, whereas he synonymized *A. laevata* and *A. granata* with *Metopotoxus laevatus* and *Cochlops muricatus*, respectively (SCOTT 1903–1904). In addition, this author referred new materials, particularly an isolated caudal armor, to *A. depressa* (but without providing an extensive rationale for his decision). He also emphasized that: “The status of this genus is somewhat uncertain and more complete material is greatly to be desired...” (SCOTT 1903–1904: 154). Finally, RUSCONI (1946: 9–11), on the basis of six associated dorsal osteoderms, recog-

nized a poorly-diagnosed new species, *A. barraelense* RUSCONI, 1946, from the Miocene of San Juan province.

Recently, the genus *Asterostemma* was reported by GOIS-LIMA & COZZUOL (2005) and COZZUOL (2006) in the upper Miocene of Acre (Brazil). Unfortunately, this Glyptodontidae material consists of one isolated osteoderm (not illustrated), and consequently its generic identification is uncertain.

SIMPSON (1947) was the first to recognize and describe a new propalaehoplophorine in more northern regions, a species from the middle Miocene of Venezuela (Santa Inés Fm.) that he tentatively assigned to the genus *Asterostemma* AMEGHINO (*A. venezolensis* SIMPSON). However, such traits as the evidently more complex morphology of the first lower molariforms, which are greatly elongated anteroposteriorly, the absence of mobile bands in the antero-lateral region of the dorsal carapace, and the particular ornamentation of the osteoderms that delimit the caudal notch, do not occur in any of the southern taxa. This situation was recognized by SIMPSON himself (1947: 9), who stated that "There remains, however, the distinct possibility that the Venezuelan specimen belongs in a distinct genus not defined from the Argentine".

Later on, DE PORTA (1962) referred some isolated osteoderms from the middle Miocene of Colombia to SIMPSON's species (*A. venezolensis*) and to *Propalaehoplophorus*, but without explicit reasons for these assignments. In 1983, VILLARROEL recognized and described a new species from the Miocene of the same country, and, like SIMPSON (1947), he assigned it provisionally to the genus *Asterostemma* (*A. ? acostae* VILLARROEL [sic]).

More recently, CARLINI et al. (1997) described a new species from the middle Miocene (Laventan) of Colombia, *A. gigantea*. Among the diagnostic characters, the large size and evident complexity of the second lower molariform, which tends to be trilobed, are remarkable. Contrastingly, molariform lobation of the southern forms is clearly defined from the third or fourth tooth. Following the ideas of SIMPSON (1947) and VILLARROEL (1983), CARLINI et al. (1997) stated that "*Asterostemma gigantea* is clearly different from species of *Propalaehoplophorus* AMEGHINO, *Cochlops* AMEGHINO, *Eucinepeltus* AMEGHINO, and *Metopotoxus* AMEGHINO. Regrettably, the carapace of the type species *A. depressa* from the early Miocene of Patagonia is very poorly known. Like VILLARROEL (1983), we cannot completely discredit the idea that the Propalaehoplophorinae from northern South America, including *A. venezolensis* SIMPSON, could belong to a new genus, distinct from *Asterostemma*. In this case, *Asterostemma* would have a geographic distribution limited to Patagonia. Into this new genus, we would include the species described herein."

Paleobiogeography and morphology of the propalaehoplophorine and glyptodontine Glyptodontidae: a new scenario

Within this paleobiogeographic and morphologic framework, a detailed analysis of the main traits that characterize the southern Propalaehoplophorinae forms indicates that most of these traits do not occur in the more northern Mio-Pliocene forms (from Colombia and Venezuela). Thus, the southern Propalaehoplophorinae are characterized by: **a)** first two upper and lower molariforms simple, with subcircular or subelliptical outline, and third molariform with slight indication of lobation in some species; **b)** in the dorsal carapace, the sulci separating the central figure from the peripherals (main sulcus) and these from each other (radial sulci) are "V"-shaped in transversal section, a morphology that is conserved in the hoplophorine Hoplophorinae; **c)** dorsal surface of the osteoderms smooth, without remarkable features and, in many cases, with anterior accessory peripheral figures; **d)** vestiges of imbrication between successive osteoderm rows in the most anterolateral region of the dorsal carapace (as in Dasypodidae; see SCOTT 1903–1904). In addition, the monophyly of the southern forms has been suggested by FERNÍCOLA et al. (2006), although the issue is problematic and there is no clear consensus about it.

As we have mentioned before, a new and more thorough examination has shown that this combination of characters does not occur in the taxa from northern South America, which have been traditionally included in subfamily Propalaehoplophorinae on the basis of the superficial similarity in the rosette ornamentation pattern of the dorsal carapace.

The type of *Boreostemma venezolensis* n. comb. (n/n) shows a notable antero-posterior elongation and greater complexity of the first two lower molariforms, absence of mobile bands in the lateral region of the carapace, and a particular ornamentation of the osteoderms adjacent to the caudal notch (SIMPSON 1947).

In *Boreostemma acostae* n. comb. (ICNUNC P-225-1) the dorsal carapace osteoderms have a strongly punctate dorsal surface, particularly in the middle of the central figure; in addition, the sulci separating the central figure from the peripherals are wide and shallow (see VILLARROEL 1983).

Other remarkable traits of *Boreostemma gigantea* n. comb. (IGM 250928) are the large body sized and a beginning of trilobation already in the second lower molariform, which is morphologically more complex than that of *B. venezolensis*, and much more so than in the southern taxa. In addition, the carapace osteoderms are thick and lack secondary peripheral figures (CARLINI et al. 1997).

Finally, *Boreostemma pliocena* n. sp. (AMUCURS 158) differs from the southern forms by the greater size and thickness of its osteoderms with strongly punctate dorsal surface, by its caudal ring osteoderms

with the central figure only slightly marked and no trace of peripheral figures, and by having the posterior upper molariforms (at least M6–M8) very close to each other with almost no separation.

In addition to this particular set of characters occurring in these taxa, a detailed examination of the morphology of the sulci that separate the central figure from the peripherals and the latter from each other shows that it differs from the condition observed in the southern taxa (in which these structures are “V”-shaped in transversal section). Indeed, in these northern taxa, the transversal section of these sulci has walls parallel to each other and an almost flat bottom. Additionally, the dorsal surface of the osteoderms is always strongly punctate, the osteoderms are thick and the area of articulation between them is notably denticulated.

This notable morphological differentiation between the Patagonian taxa and those from northern South America agrees with the paleobiogeographic scenario outlined by CARLINI et al. (1997) for the middle Miocene. These authors have proposed other possible evolutionary scenarios for the Cingulata at lower latitudes, given the distant phylogenetic relationship between the taxa in both areas, among other elements. The Dasypodidae that are present in northern regions include the Astegotheriinae, Dasypodini, and Tolypeutinae, which are absent in Patagonia; on the contrary, the Peltephilini, Euphractini, and Stegotheriini occur in the latter area (CARLINI et al. 1997). Accordingly, VIZCAÍNO et al. (1990) have suggested a probable intertropical origin for the dasypodine Dasypodidae.

Within the Glyptodontidae, the subfamily Glyptodontinae maintains this primitive pattern of rosette ornamentation (“Araucanian” – Lujanian) (see AMEGHINO 1889; HOFFSTETTER 1958; PASCUAL et al. 1966; PAULA COUTO 1979). In fact, some authors (e.g., CABRERA 1944) have highlighted the notable similarity in dorsal carapace ornamentation between the earliest Glyptodontinae species (*Glyptodontidium tuberifer*; see CABRERA 1944) and the Propalaeohoplophorinae. However, in the Glyptodontinae, as in the *Boreostemma* species, the sulci are not parabolic in transversal section, but have parallel sides and a flat bottom (“U”-shaped); this detail has already been noted by authors such as CASTELLANOS (1953) for *Paraglyptodon*. This is coupled to the fact that the dorsal surface of the osteoderms is strongly punctate in the earliest Glyptodontinae (CABRERA 1944; CASTELLANOS 1953), whereas, in the terminal taxa (*Glyptodon* OWEN 1839 and *Glyptotherium* OSBORN 1902), this surface is rugose, with deep and wide sulci (BURMEISTER 1870–1874; AMEGHINO 1889; SOIBELZON et al. 2006; CARLINI et al. 2008).

To sum up, the following trends seem to occur in the glyptodontine Glyptodontidae: **a)** progressive increase of the width and depth of the sulci dividing the central figure from the peripherals; these always with parallel sides and a flat bottom; **b)** increasing rugosity of the dorsal surface of osteoderms, which is openly ru-

gose in the terminal taxa, without secondary peripheral figures; **c)** increasing osteoderm thickness; **d)** tendency of the articulation between osteoderms to become highly denticulated; **e)** lobation of first upper and lower molariforms. The first molariform is already trilobated in *Glyptodon* (see SOIBELZON et al. 2006).

Discussion

The Miocene Glyptodontidae of northern South America (Colombia and Venezuela) have traditionally been included within the Propalaeohoplophorinae, and, more precisely, assigned to the genus *Asterostemma*, a taxon originally recognized from Argentinian Patagonia. However, the rosette ornamentation pattern of the dorsal carapace osteoderms (which represented the main basis for these assignments) of southern Propalaeohoplophorinae is not the same as that of the northern taxa that were originally assigned to this subfamily. In effect, as we stated, while the sulci shows a “V”-shaped transversal section in the Propalaeohoplophorinae and hoplophorine Hoplophorinae, this transversal section is clearly “U”-shaped in the taxa from Colombia and Venezuela. This is coupled to greater complexity of the anterior molariforms, and possession of dorsal osteoderms with extremely punctate dorsal surface, greater thickness, and markedly denticulated articulation surfaces.

This morphologic differentiation between “southern” and “northern” forms agrees with the paleobiogeographic and evolutionary scenario proposed by SCILLATO-YANÉ (1986) and CARLINI et al. (1997) for the cingulate Xenarthra, which was also indirectly anticipated by SIMPSON (1947) and VILLARROEL (1983), given the particular differences observed between most Cingulata from these two areas. As we have previously discussed, in this context, the characters observed in *Asterostemma venezolensis*, *A. ? acostae*, and *A. gigantea* justify their exclusion from the genus *Asterostemma* and the Propalaeohoplophorinae, and their assignment to our new genus *Boreostemma*. Furthermore, this set of evidences strongly suggests that these taxa represent the first stages in the cladogenesis of the glyptodontine Glyptodontidae.

In agreement with this, the biogeographic and phylogenetic history of the Glyptodontinae was poorly known until now, and it was practically restricted to the southernmost regions of South America. Within this area, their Tertiary records are scarce, relatively late, and show characters typical of the terminal Pleistocene glyptodontines, which suggests that these are already derived taxa.

Thus, the first record of a Glyptodontinae corresponds to *Glyptodontidium tuberifer* from the “Araucanian” (late Miocene – early Pliocene) of NW Argentina (CABRERA 1944). The stratigraphic provenance of this taxon is somewhat uncertain, given that the “Araucanian” is represented by the Andalhuala and Corral Que-

mado formations. However, some datings have suggested that the Andalhuala Fm. could correspond to 7 – 3.54 Ma (BUTTLER et al. 1984; BOSSI et al. 1987; BOSSI & GAVRILOFF 1998; GAVRILOFF 2000; HERRERA & ORTIZ 2005). Likewise, the Corral Quemado Fm. is close to 3.54 Ma in age (BUTTLER et al. 1984); however, datings from the base of this formation range between 4.61 and 4.83 Ma (STRECKER et al. 1989; BOSSI & GAVRILOFF 1998), while the most modern ones correspond to about 2.9 Ma (BOSSI & GAVRILOFF 1998) or are even younger (2.4 Ma?; [sic] BOSSI et al. 1987).

The other Tertiary Glyptodontinae genus is *Paraglyptodon* CASTELLANOS (Pliocene, Chapadmalalan – Marplatán) (see ROVERETO 1914; CASTELLANOS 1953) from South America. One species of this genus (*P. chapadmalensis* AMEGHINO, 1908) is biostratigraphically important, since it is characteristic of the upper Chapadmalalan Age/Stage (ca. 3.5 – 3.2 Ma.) (see CIONE & TONNI 2005). Similarly, the distribution of *P. uquiensis* seems to be restricted to the latest Chapadmalalan and the Marplatán (REGUERO et al. 2007).

A remarkable species diversification occurred among the Glyptodontinae during the Pleistocene (ca. 1.8 – 0.008 Ma), along with a wide geographic distribution that was probably stimulated by the expansion of open environments during the glacial periods (CLAPPERTON 1993; CIONE et al. 2003; RABASSA et al. 2005). In fact, these are probably the only Glyptodontidae to successfully partake in the GABI, given that they occur in North America since the early Blancan (ca. 3.9 Ma) (CARRANZA-CASTAÑEDA & MILLER 2004), and evolved several taxa in that subcontinent, from the late Blancan (ca. 2.6 Ma) to the Rancholabrean (late Pleistocene) (GILLETTE & RAY 1981; WHITE & MORGAN 2005; MORGAN & WHITE 2005; CARLINI et al. 2008) (but see DOWNING & WHITE 1995).

To sum up, the evidence indicates that the Mio-Pliocene taxa from Colombia and Venezuela are not Propalaehoplophorinae, but share several derived characters with the glyptodontine Glyptodontidae. Hence it is possible to propose a partial reinterpretation of the phylogenetic and biogeographic history of the Glyptodontinae. Indeed, until the recognition of *Boreostemma* n. gen. in the present contribution, the oldest records of Glyptodontinae (late Miocene – Pliocene) were restricted to southern South America (Buenos Aires, Catamarca and Jujuy provinces, Argentina) and suggested a southern differentiation for the subfamily, probably from advanced Propalaehoplophorinae (CARLINI et al. 1997).

On the contrary, the new evidence presented here strongly suggests that the origin of the Glyptodontinae was geographically located in northern South America and much earlier (middle Miocene) than previously supposed, since the reliable records from the Honda Group, Colombia (*Boreostemma gigantea* and *B. acostae*), date from approximately 13 Ma (CARLINI et al. 1997; KAY et al. 1997).

Suggestively, the first Glyptodontinae records (*Glyptodontidium tuberifer*) in southern South America coincide with what PASCUAL & BONDESIO (1982) called “Age of Southern Plains”, which includes the Chasicuan, Huayquerian, Montehermosan, and Chapadmalalan ages (ca. 11 – 3 Ma) (see PASCUAL et al. 1996) and whose beginnings were undoubtedly related to the Quechua Phase of Andean Orogeny (see YRIGOYEN 1979). More precisely, the evidence suggests that the first southern Glyptodontinae records correspond to the latest Miocene or Pliocene, when these great plains reached their maximum development (ORTIZ JAUREGUIZAR 1998), extending from north Patagonia to Venezuela (MARSHALL et al. 1983; ORTIZ JAUREGUIZAR & CLADERA 2006). In fact, some authors have suggested that these climatic-environmental conditions greatly favored the entrance of the first Holarctic immigrants, which already show clear adaptations to open grassland environments (e.g., Cricetidae and Tayassuidae) (VUCETICH 1986; MENEGAZ & ORTIZ JAUREGUIZAR 1995; PARDIÑAS 1995). Thus, it is possible that these great open extensions also favored the dispersion of the glyptodontines into more southern areas through “biogeographical corridors”.

The recognition of this new genus and species in northern South America, and the associated systematic and paleobiogeographical consequences, highlight the importance of research in continental sediments at these latitudes, especially considering the proximity to areas that functioned as biogeographic corridors between both American subcontinents (WOODBURNE et al. 2006). These corridors modified the biotic relationships in both Americas, especially in South America, which had almost insular characteristics during a large part of the Cenozoic.

Conclusions

1. The morphological evidence indicates that the propalaehoplophorine Glyptodontidae as previously defined (southern taxa plus taxa from northern South America) are not a natural group.
2. Consequently, we propose the recognition of a new genus (*Boreostemma*) for the Venezuelan and Colombian species previously assigned to *Asterostemma*, while the latter taxon is geographically restricted to Argentina.
3. *Boreostemma* includes the following species: *B. acostae* (VILLARROEL 1983) and *B. gigantea* (CARLINI et al. 1997) from the middle Miocene of La Venta, Colombia, and *B. venezolensis* (SIMPSON 1947) and *B. pliocena* n. sp. from the Miocene and Pliocene of Venezuela, respectively.
4. The characters of this new genus and the species referred to it (e.g., sulci between central and peripheral osteoderms “U”-shaped in transversal section, dorsal surface of osteoderms in the dorsal carapace highly punctate, greater osteoderm thickness, osteoderm articulation highly denticulated and with evident pro-

longations, anterior molariforms complex), suggest the inclusion of these taxa among the glyptodontine Glyptodontidae, which are rare in the fossil record of southern South America for that period.

5. Consequently, it is possible to hypothesize that this genus represents the start of the cladogenesis of glyptodontine Glyptodontidae, which seems to have taken place in much more northern regions than previously supposed. It is also possible that the arrival of these Glyptodontinae to southern South America was favored by the emergence of large open savanna environments during the "Age of Southern Plains".
6. The propalaeophorine Glyptodontidae are restricted to the Oligo-Miocene of the southern cone of South America, mainly in Patagonia.

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